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A surprising new genus and species of cave-adapted Plusiocampinae *Cycladiacampa irakleiae* (Diplura, Campodeidae) from Irakleia Island, Cyclades Islands in the Aegean Archipelago (Greece)

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Abstract

The surprising discovery of *Cycladiacampa irakleiae*, a new genus and species, a cave-adapted campodeid dipluran highlights the paleobiogeographical importance of the insular Aegean cave-ecosystems. This new dipluran genus inhabits with other noticeable endemic cave-adapted invertebrate species in the isolated Spilaio Agiou Ioanni cave in Irakleia, a small island in the centre of the Cyclades Archipelago. *C. irakleiae* **gen. nov. et sp. nov.** is related with *Stygiocampa* species, a subgenus of *Plusiocampa* genus, with hereto six cave-adapted species inhabiting karst areas in Dinaric and the Rhopode Mountains. These species share similarities such as the absence of mesonotal and metanotal macrosetae, the abundance and shape of uros-

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ternal macrosetae, as well as the lack of medial posterior macrosetae on mesonotum and metanotum. This can be explained by a common ancestor that probably originated from Asia and expanded its distribution to the fragmented Europe since the Eocene-Oligocene, colonizing cave habitats in recent periods. *Cycladiacampa irakleiae* is a remarkable addition to the fauna of the cave of Irakleia and should raise awareness on the need to enhance the study and conservation of the cave's natural heritage.

Keywords
Campodeidae, troglobite, fauna, new species, biogeography

Introduction

The Aegean Archipelago, which has more than 9,800 islands and islets in an area of 215,000 km^2, is the largest archipelago of the Mediterranean Sea, and it is one of the archipelagos with the highest number of islands worldwide (Blondel et al. 2020). Standing at the intersection of Europe, Asia, and Africa, it is characterized by a complex palaeogeographical history and high levels of biodiversity and endemism (Triantis and Mylonas 2009, Sfenthourakis and Triantis 2017). Soil and cave dwelling dipluran species in the Aegean Archipelago (Silvestri 1912, 1933, Pagés 1953, Condé 1984, Sendra et al. 2020) include 26 species from two of the ten most diverse families of these basal hexapods: Campodeidae and Japygidae. The family Campodeidae represented by 14 species: six widespread soil species of *Campodea* Westwood, 1842, two species with limited range (*Edriocampa ghigii* Silvestri, 1933 and *Eutrichocampa aegea* Silvestri, 1933), and six species of *Plusiocampa* Silvestri, 1912 (these inhabiting from soil to cave habitats and including two recently described cave-adapted species *Plusiocampa* (*Plusiocampa*) *hoffmanni* Sendra & Paragamian, 2020 and *Plusiocampa* (*Plusiocampa*) *chiosensis* Sendra & Gasparo, 2020). Japygidae are represented by 12 soil-dwelling species from two genera with limited range *Megajapyx* (Verhoeff, 1904) and *Parindjapyx* Silvestri, 1933, and two widespread genera *Metajapyx* Silvestri, 1933 and *Japyx* Haliday, 1864.

Within the Aegean Archipelago, Irakleia is a small island (area ~17 km^2, max elv. 418 m a.s.l., coastline 29.2 km) of the Cyclades Archipelago situated approximately 33 km south of the port of Naxos Island and 5,3 km from its southernmost coast (cape Katomeri). There are two settlements (Panagia and Agios Georgios), with 141 inhabitants (2011 national census). The island is dominated by areas with low sclerophyllous vegetation, followed by sparsely vegetated areas, abandoned terraces, and arable land. The climate is typically Mediterranean with mild winters and hot, dry summers. The average annual temperature is 17.7 °C, and the average annual rainfall is 340 mm (http://penteli.meteo.gr/stations/iraklia/).

No published data on diplurans is available for Irakleia (Cyclades, Greece), but during a recent survey in a cave a new Plusiocampinae genus and species were collected. This represents a remarkable addition to the astonishing cave fauna of this small island and a new insight into the colonization of cave-ecosystems in the eastern Mediterranean karst regions.

Material and methods

The specimens stored in ethanol 96%, were washed using distilled water, mounted on slides with Marc André II solution, and examined under a phase-contrast optical microscope (Leica DMLS). The illustrations were made with a drawing tube, and measurements were taken with an ocular micrometer. Measure of the body length was taken on specimens mounted *in toto*, and measured from the base of the frontal process distal macrochaetae to the abdomen's supra-anal valve. Two specimens coated with palladium-gold were used for SEM (Hitachi S-4100) photography and to measure the sensilla.

The morphological descriptions and abbreviations follow Condé (1956). We use the term gouge sensilla for the concavo-convexly shaped sensilla on the antennae (Bareth and Condé (1981). For the position of macrosetae we adopt the abbreviations of Condé (1956): *ma*, medial-anterior *la*, lateral-anterior, *lp*. lateral-posterior and *post*, posterior.

Results

Taxonomy
Class Hexapoda Blainville, 1816
Order Diplura Börner, 1904
Suborder Rhabdura Cook, 1896
Family Campodeidae Lubbock, 1873
Subfamily Plusiocampinae Paclt, 1957

***Cycladiacampa* Sendra, gen. nov.**
http://zoobank.org/06F78C51-13C1-4404-874D-6D36CD614CB1

Type species. *Cycladiacampa irakleiae* Sendra, sp. nov.

Etymology. *Cycladiacampa* is a compound name comprising of "Cycladia", referring to the large insular landmass created by a major drop of the sea level during last glacial maximum (23–18 ka) at the site of the modern Cyclades Islands, and the suffix "-campa", traditionally used in Campodeidae taxonomy. Gender: feminine.

Diagnosis. On pronotum 1+1 *ma*, 2+2 $la_{1,3}$ and 2+2 $lp_{1,3}$, on meso- and metanotum without macrosetae (Figs 5, 6); one dorsal femoral macrosetae and one sternal tibial macrosetae; unequal claws in size with lateral-crests (Figs 11–13); thick setiform pretarsal lateral processes covered with long barbs except in the final part (Figs 11–14); male and female have thin subcylindrical appendages that carry glandular a_1 setae (Figs 15, 16, 18); the male has a large field of glandular g_1 setae in the slightly expanded posterior urosternite border (Fig. 16); the female is without this glandular field (Figs 15, 18). There are up to 1+1 *la* and 5+5 *post* macrosetae on IV–VII urotergites; 11+11–10+10 macrosetae on urosternites I–VII and 2+2 macrosetae on VIII (Figs 15–17, 19, 20).

***Cycladiacampa irakleiae* Sendra, sp. nov.**
http://zoobank.org/A1FC59A1-8600-4579-99D8-0850CE7BD5FD
Figs 1–21; Table 1

Etymology. The specific epithet *irakleiae* refers to the island it was found on.

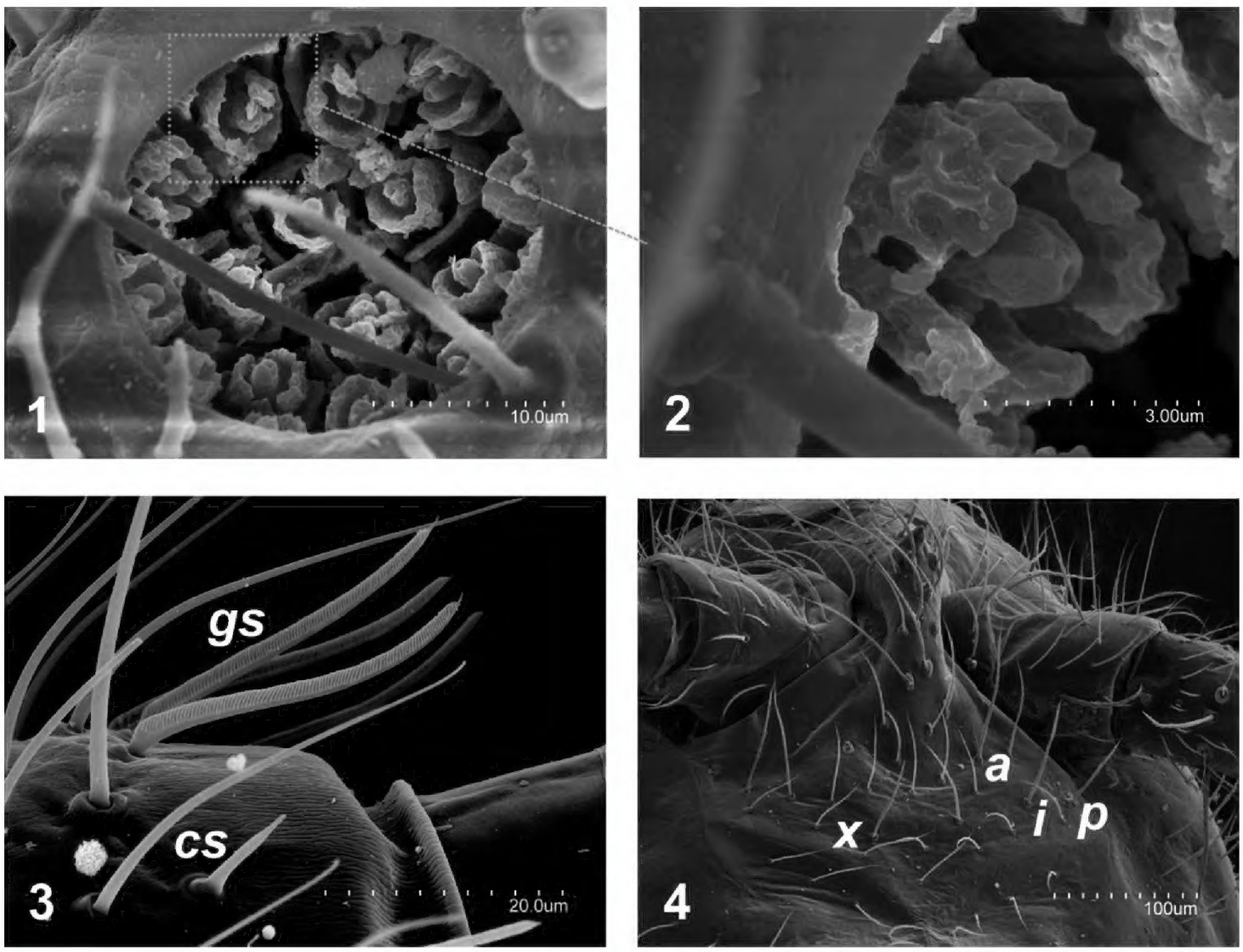
Type locality. Greece, Cyclades Islands, Irakleia Island: Spilaio Agiou Ioanni cave or Irakleia cave, (36°49'43.74"N, 25°26'12.48"E, 110 m a.s.l.).

Type material. Male holotype labelled M1-03400 is from Spilaio Agiou Ioanni cave, Notio Aigaio, Irakleia, Irakleia Island, Greece, 22th May 2019, I. Nikoloudakis leg. Two young males, one young female, and one adult female paratypes are labelled M2-03400, M3-03400, H2-03400, and H1-03400, respectively; they are from the same cave, date and collector. Three males and five females paratype labelled M1 to M3-02817 and H1 to H5-02817, respectively, are from the same cave, but they were collected using pitfall traps installed between 26th November 2016 and 26th February 2017, leg. I. Gavalas. All type material was mounted in Marc André II solution, deposited in MZB, Museu de Zoologia de Barcelona, Spain (labelled holotype M1-3400), Coll. AS, private collection of Alberto Sendra, València, Spain (M1 to M3-02817 and H1 to H5-02817), and MHNG, Muséum d'histoire naturelle de Genève (paratypes M2-03400, M3-3400, H2-03400, H1-03400).

Other studied material. Two specimens from the same cave, and with the same data and collector as the holotype. These were mounted on two separate aluminium stages and coated with palladium-gold.

Description. ***Body.*** Body length 2.5–3.9 mm (males, n = 6), 3.3–6.1 mm (females, n = 7) (Fig. 21, Table 1). The epicuticle is smooth under optical microscope, but under high magnification, it is weakly reticulated, showing irregular and roundish polygonal structures of variable sizes (Figs 7, 8); the body has slightly long, thin clothing setae with thin barbs along distal two–thirds of each seta.

Head. Antennae have 47 antennomeres in three completed and intact antennae; the antennae are approximately ~1.5 times longer than the body's length, with medial antennomeres two or three times longer than wide and apical antennomere three times longer than wide (Table 1). The cupuliform organ has about 18 complex olfactory chemoreceptors, and each one has two multiperforated concentric folds around a coniform central structure (Figs 1, 2). The distal and central antennomeres have two or three whorls of smooth macrosetae and scattered smooth setae, in addition to a single distal whorl of 8–10 moderately long gouge sensilla (25–30 μm long), and up to two very short coniform sensilla 10–12 μm long (Fig. 3). The proximal antennomeres have typical trichobothria, plus a small coniform sensillum on the third antennomere in ventral position. The frontal process has a moderate coniform protrusion that is covered with few tuberculate setae and a few thin barbs (Fig. 4). The three macrosetae along each side of the insertion line of antennae and *x* setae have thin distal barbs; The length ratios of *a/i/p/x* are 39/28/26/23, respectively, in holotype (Fig. 4). The labial palps are suboval with small latero-external sensillum, two guard setae, up to six setae on anterior border, and up to 64 neuroglandular setae in holotype.



Figures 1–4. *Cycladiacampa irakleiae* Sendra, sp. nov. **1** apical view of last antennomer with cupuliform **2** olfactory chemoreceptor of the cupuliform organ **3** lateral distal view of central antennomer with gouge sensilla **4** frontal process. (*gs*= gouge sensillum; *cs*= coniform sensillum; *a*= anterior-macroseta, *i*= intermediate macroseta, *p*= posterior-macroseta, *x*, *x*-setae).

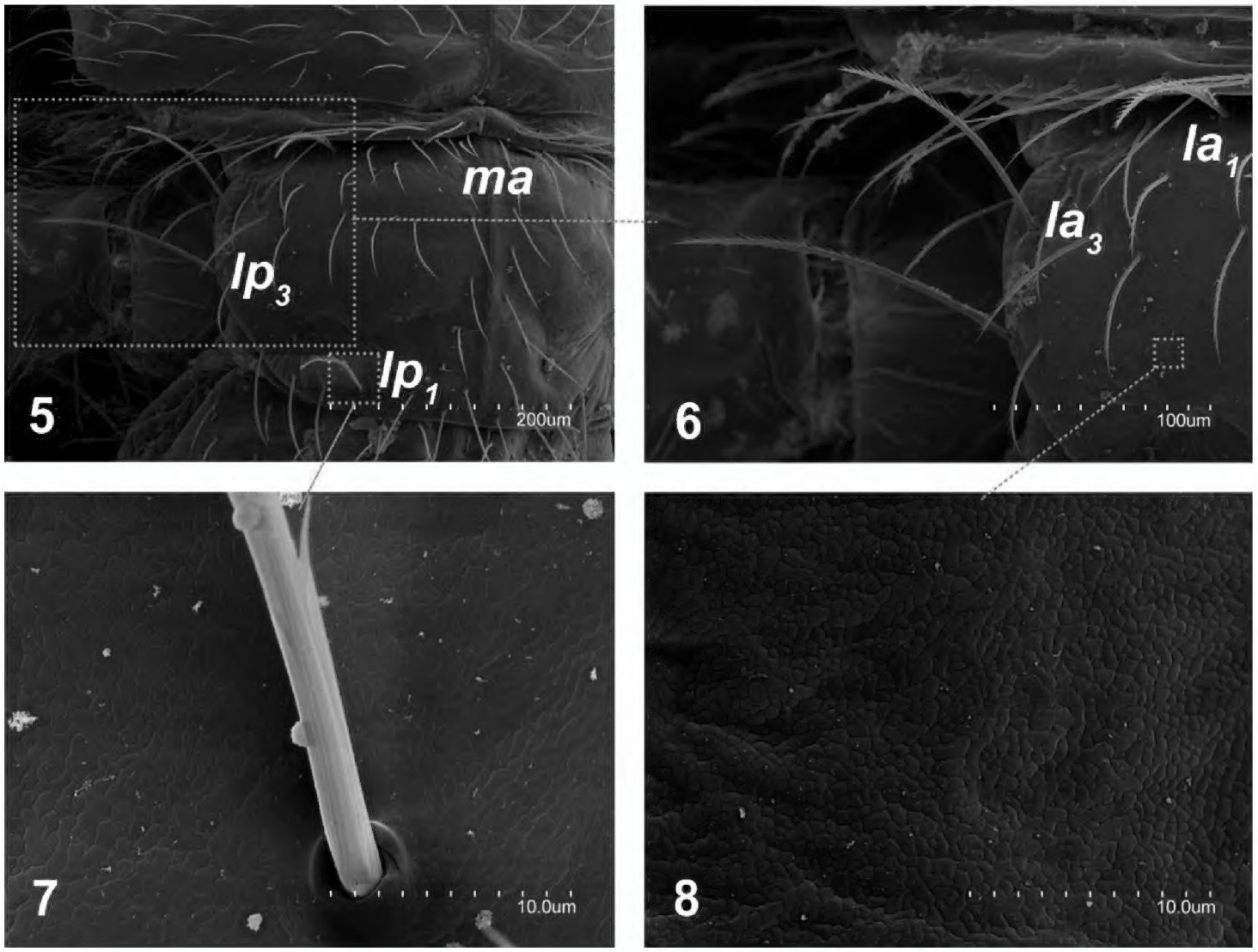
Thorax. The thoracic macroseta distribution (Figs 5, 6): pronotum with 1+1 *ma*, 2+2 $la_{2,3}$, 2+2 $lp_{2,4}$ macrosetae; mesonotum and metanotum without macrosetae. All macrosetae are long and with thin barbs along basal half to two-thirds of their length; thin marginal setae double the length of the clothing setae, and both have thin distal barbs (Figs 5, 6). The legs are elongated, and the metathoracic legs overpass the end of the abdomen; young adults have relatively longer legs than the largest adults (Table 1). The tibia is always longer than the femur or tarsus (Table 1, Figs 9, 10). Femora I–III have one well-differentiated long dorsal macrosetae each (0.15 mm in holotype) with thin long barbs on the distal four fifths. The calcars have long, thin barbs all over. Tibia I–III have one well-barbed ventral macrosetae. Tarsus have numerous setiform setae along and two dorsal subapical setae similar barbed than clothing setae but much longer (Figs 9–11). The claws are unequal in size, that is, the posterior claw is longer than the anterior claw (1.4–1.5: ratio posterior/anterior). The claws have large lateral crests and their ventral side are noticeably ridged and covered with a micro-granulated surface; the posterior claw is large with a backward overhang (Figs 11–13). The pretarsus has a thick setiform lateral

Table 1. *Cycladiacampa irakleiae* Sendra sp. nov., length of the body, antennomer metathoracic leg and their segments, and cerci (units in mm); number of antennomeres and cercal articles.

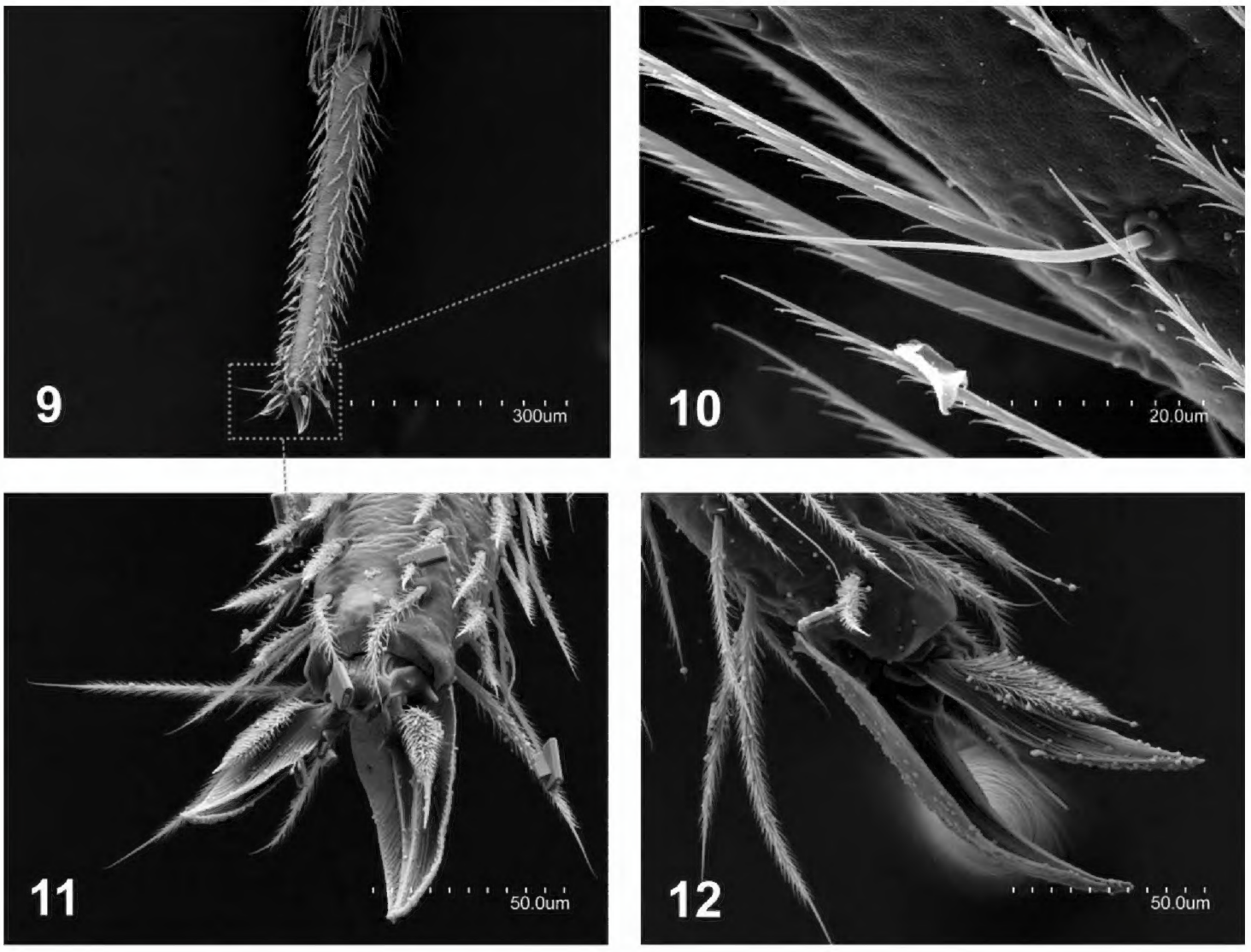
		Antennae		Metathoracic leg					Cercus										
Specimen	**Body**	**Length**	**Number of antennomeres**	**Trochanter**	**Femur**	**Tibia**	**tarsus**	**Total leg**	**Divisions of the basal article**	**Basal article**	**1st**	**2nd**	**3tr**	**4th**	**5th**	**6th**	**7th**	**Total cercus**	**Number of cercal articles, basal included**
M2-03400 (young) paratype	2.50	–	–	0.10	0.63	0.75	0.58	2.06	–		–	–	–	–	–	–			–
M3-03400 (young) paratype	2.90	4.40	47	0.15	0.60	0.75	0.55	2.05	7	2.50	0.51	0.90	1.10	1.22	1.35			7.58	6
H2-03400 (young) paratype	3.30	4.65	47	0.15	0.65	0.80	0.60	2.20	–	–	–	–	–	–	–	–			–
M2-02817 paratype	3.40	–	–	0.18	0.72	0.92	0.71	2.53											
M3-02817 paratype	3.50	–	–	0.16	0.80	1.01	0.76	2.73	–	–	–	–	–	–	–	–			–
M1-03400 holotype	3.8	–	–	0.15	0.95	1.15	0.75	3.00	8	2.25	0.50	0.70	0.92	1.10	1.25	1.32	1.20	9.24	8
M1-02817 paratype	3.9	–	–	0.13	0.75	0.98	0.73	2.59	–	–	–	–	–	–	–	–	–		–
H1-02817 paratype	4.3	–	–	0.20	0.86	1.06	0.78	2.90											
H1-03400 paratype	4.7	7.05	47	0.20	1.05	1.30	0.85	3.40	–	–	–	–	–	–	–	–	–		–
H2-02817 paratype	5.4			0.30	1.25	1.45	0.97	3.97											
H3-02817 paratype	5.7			0.25	1.12	1.47	1.01	3.85											
H4-02817 paratype	5.9			0.29	1.05	1.47	0.98	3.79											
H5-02817 paratype	6.1			0.27	1.17	1.45	0.98	3.87											

processes covered around with abundant and dense barbs that are bent at the ends almost all over except in the distal part (Figs 11–14).

Abdomen. Distribution of abdominal macrosetae on tergites: 1+1 *la* (exceptionally 0+1 $post_5$) on IV; 1+1 *la*, 1+1 $post_5$ on V, 1+1 *la*, 3+3 (2+3) $post_{3,4,5}$ on VI, 1+1 *la*, 5+5 $post_{1\text{-}5}$ on VII: 7+7 (8+8) $post_{1\text{-}7}$ on VIII; and 12+12 (13+13) *post* on IX abdominal segment. All tergal abdominal macrosetae are long and well-differentiated with thin barbs along the distal half to four fifths. Urosternite I with 11+11 well-barbed macrosetae (Figs 15, 16); urosternites II to VII with 10+10 (11+11) macrosetae (Fig. 17); urosternite VIII with 2+2 macrosetae (Fig. 20); urosternal macrosetae are of medium length or longer and have long barbs all around along the distal four fifths. The stylus has an apical, subapical and ventromedial seta completely covered with barbs all around except at the ending part (Figs 17, 19, 20). The two apparently intact cerci are respectively 2.6 and 2.4 times de body length; they have five and seven primary articles apart from the multi-divided basal article (Table 1). The length of the cerci increases from the proximal to distal articles. Each article has a variable number of untidy whorls of thin barbed macrosetae increasing from proximal to distal primary article. All primary articles have a distal short, thin, barbed whorl seta.



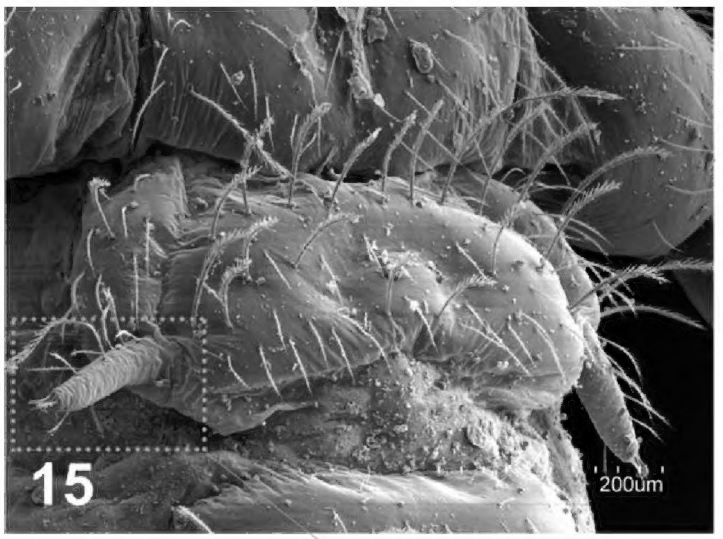
Figures 5–8. *Cycladiacampa irakleiae* Sendra, sp. nov. **5** posterior part of the head to anterior part of mesothorax, left side, with pronotal macrosetae (*ma*, *la*, *lp*) **6** lateral left side of prothorax with *la* and *lp* macrosetae **7** detail of the surface of pronotum with insertion of lp_1 macrosetae **8** detail surface of pronotum.

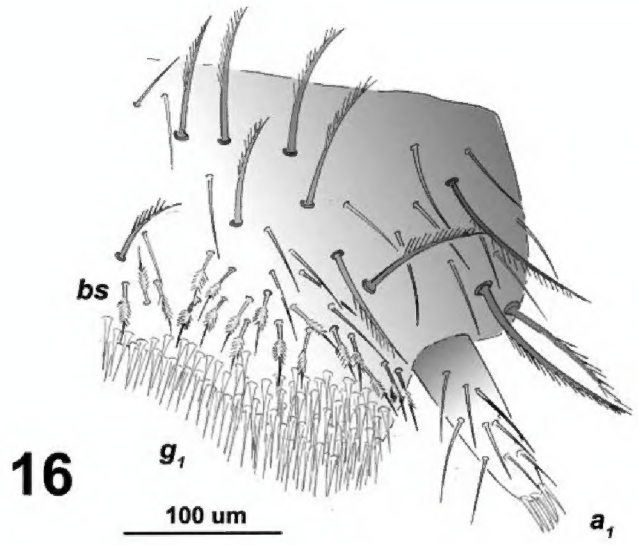


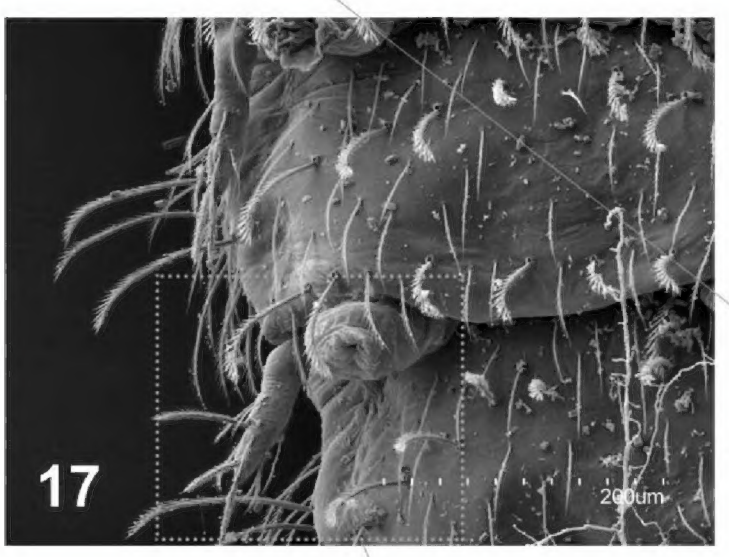
Figures 9–14. *Cycladiacampa irakleiae* Sendra, sp. nov. **9** distal part of tibia, plus tarsus and pretarsus of metathoracic leg **10** detail of tarsus, lateral side, with a setiform sensillum (*ss*) **11** pretarsus of metathoracic leg, ventral side **12** pretarsus of metathoracic leg, lateral side **13** pretarsus of metathoracic leg, detail ventral side **14** detail of lateral processes.

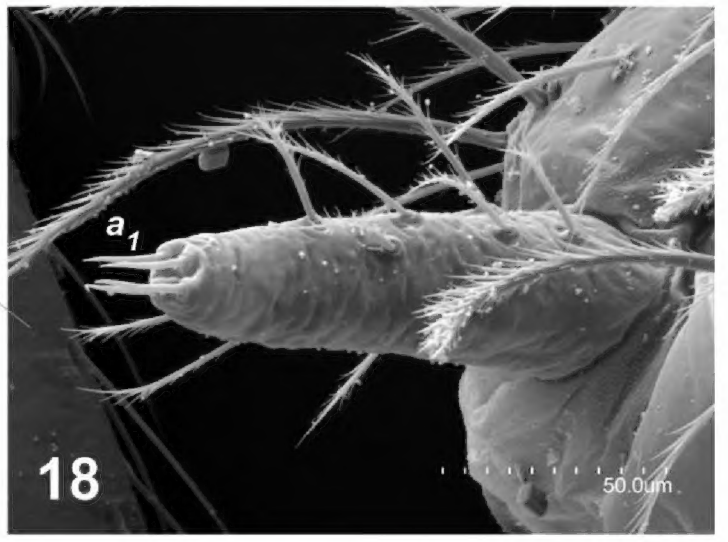
Secondary sex characters. Female urosternite I have short coniform appendages, bearing each up to five glandular a_1 setae in a apical field (Figs 15, 18).

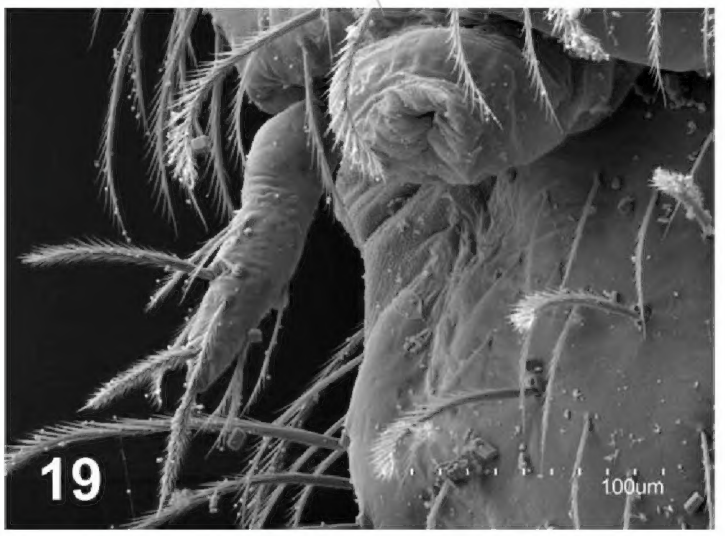
Male urosternite I have short coniform appendages, bearing each about six glandular a_1 setae in a apical field; the posterior edge is slightly enlarged at both sides of the

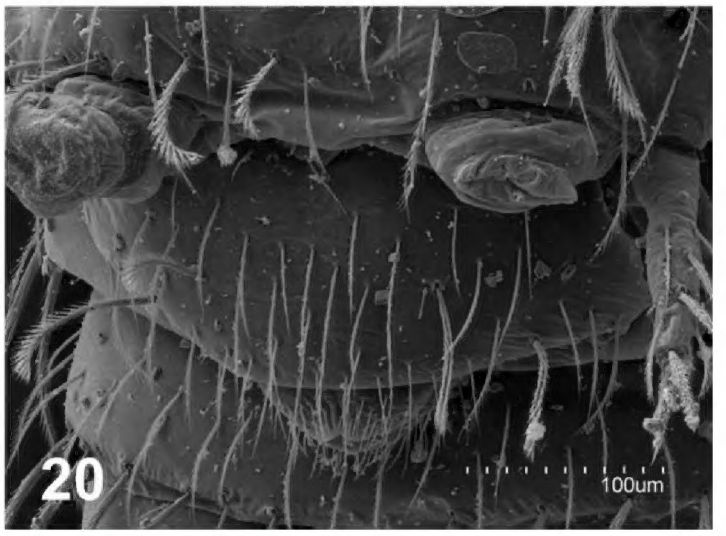












Figures 15–20. *Cycladiacampa irakleiae* Sendra, sp. nov. **15** first urosternite of a female **16** first urosternite of holotype, male, left side **17** fourth urosternite, right side **18** detail of the right appendage of the first urosternite of a female **19** detail of the fourth urosternite, right side **20** posterior part of seventh and the complete eighth urosternites.

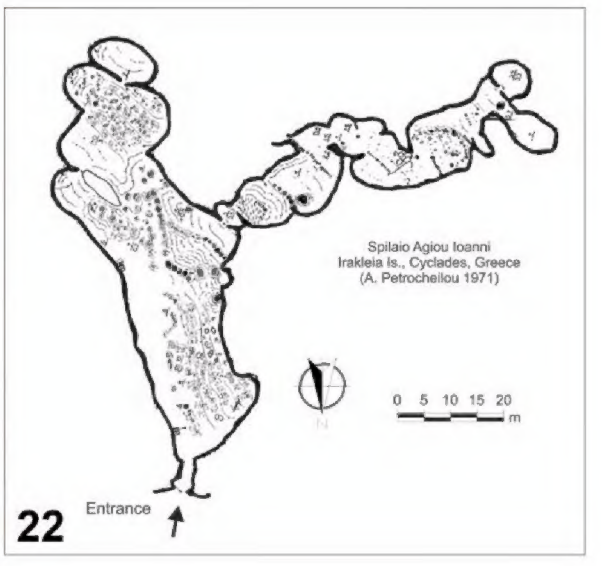
first urosternite, with a glandular field of up to 190 glandular g_1 setae arranged from five in lateral to two in the centre of this posterior glandular field; in addition, in an anterior position there are about 40 short setae clearly different from clothing setae for their middle well-barbed part (Fig. 16).

Cave description

Spilaio Agiou Ioanni cave is located on the southwestern part of Irakleia Island at 110 m a.s.l. A 2.5 km marked path leads from the Panagia settlement to its entrance. The entrance is relatively narrow (height: 0.5–0.7 m, width: 1.5–1.7 m) (Figs 22, 24) and reaches a large chamber (27 m long, 17 m wide and up to 10 m high) (Figs 22, 23). The cave is heavily decorated with a variety of speleothems. There are two main large chambers and several smaller ones, measuring 170 m in total length and covering an area of 2,000 sq. m (Petrocheilou 1971) (Fig. 22).

The fauna of Irakleia cave

The fauna of the cave is known from material collected by P. Beron & A. Bartsiokas, (on 14.09.1981), B. Hauser (on 11.05.1985 and 26.04.1987), I. Gavalas (in several



Figures 21–24. 21 *Cycladiacampa irakleiae* Sendra, sp. nov habitus (photo: I. Gavalas) **22** map of the cave of Irakleia, modified from Petrocheilou (1971); most of the specimens of *Cycladiacampa irakleiae* n.gen., n.sp. were collected in the western part of the cave **23** the first large chamber of Spilaio Agiou Ioanni cave (photo: I. Gavalas) **24** the narrow entrance of Spilaio Agiou Ioanni cave, Irakleia, Cyclades (photo: I. Gavalas).

visits between 2016 and 2019), and I. Nikoloudakis (on 22.05.2019). The findings have been cited from time to time in: Beron (1985), Andreev (1986), Condé (1987), Matic and Stavropoulos (1988), Mendes (1988), Osella (1989), Condé (1990), Besuchet (1993), Tanasevitch (2011), Beron (2016), Naumova et al. (2016), and Paragamian et al. (2018). A checklist is regularly updated in the Cave Fauna of Greece Database (Paragamian et al. 2020). Despite its small size, the cave Spilaio Agios Ioannis has a remarkable fauna of 19 valid invertebrate species recorded so far. At least five species are endemic to the cave: the troglophile beetle *Absoloniella nitidipennis* (Osella, 1989), that probably also occurs outside the cave, and the cave-adapted troglobionts, such as the palpigrad *Eukoenenia naxos* Condé, 1990, the staphylinid beetle *Antrobythus perplexus* Besuchet, 1993, the zygentoma *Protrinemura mediterranea* Mendes, 1988, and the newly discovered *Cycladiacampa irakleiae* gen. et sp. nov. (Diplura, Campodeidae). Two of the caves's other troglobiont species, the peudoscorpion *Hadoblothrus aegaeus* Beron, 1985 and *Chthonius schmalfussi* Schawaller, 1990, were also found in a cave in Santorini Island (South Cyclades). Beside the surprising finding of *C. irakleiae* gen. et sp. nov., the finding of *P. mediterranea* is noteworthy as there are only three more species of the genus existing at very disjunctive ranges: one in eastern China, one in Thailand, and one in Ryukyu Islands (Japan) (Mendes 2018). Furthermore, new species are expected to be described in the future, as for example the snail *Lindbergia* aff. *pseudoillyrica* (Riedel 1990, 1992), a polydesmid milliped *Brachydesmus* or *Serradium* (Andreev 1986), among others.

Discussion

Phyletic affinities

Surprisingly, a new genus of Plusiocampinae, with a unique combination of setiform and well-barbed lateral processes on the pretarsus, as well as lacking macrosetae on mesonotum and metanotum, has been discovered in an isolated karst area in a small island, Irakleia, of the Aegean Sea. *Cycladiacampa irakleiae* gen. nov. et sp. nov. has Plusiocampinae features such as pretarsus with lateral crests, abundant posterior urosternal macrosetae, and the synapomorphic feature of the pronotum with not less than 1+1 *ma*, 1+1 *la* and 2+2 *lp* macrosetae (Condé 1956, Paclt 1957, Sendra et al. 2020).

The peculiar shape of the lateral processes of the pretarsus in *C. irakleiae* sp. nov. (Figs 11–14) has similarities with the recently proposed *Whittencampa* Sendra & Deharveng, 2020, a monospecific genus with one highly troglomorphic species from caves in Guangxi, southern China (Sendra and Deharveng 2020). Nevertheless, *Whittencampa* is clearly separated from the new genus due to the processes completely covered with barbs, the presence of macrosetae on mesonotum and metanotum (absent in *C. irakleiae*), the two dorsal femora macrosetae (one in *C. irakleiae*) and, the 1+1 macrosetae on eighth urosternite (2+2 in *C. irakleiae*). Also, *Hystrichocampa* Condé, 1948, a monospecific genus from caves located in Jura karst mountains between France

and Switzerland, shows some resemblance in the lateral processes but with shorter and thinner barbs instead of longer barbs. It differs from *C. irakleiae* by the presence of abundant mesonotal and metanotal macrosetae, which are absent in *C. irakleiae*, and the five dorsal femora macrosetae, against one in *C. irakleiae*.

At present, Plusiocampinae has 112 species which are assigned to 12 genera (Sendra et al. 2020, Sendra and Deharveng 2020). The pattern of macrosetae in Plusiocampinae is characterized by a numerical increase of lateral anterior and lateral posterior macrosetae on nota, including frequently on medial posterior and rarely on medial intermediate and lateral intermediate macrosetae in mesonotum and metanotum; usually there are abundant posterior macrosetae on urotergites, with several species having extra macrosetae on the first and less frequently on the second to eighth urosternites (Condé 1956, Sendra et al. 2020). However, within Plusiocampinae, it can also be found a less frequent reduction of notal macrosetae in species of *Stygiocampa* Silvestri, 1934 subgenus of *Plusiocampa* Silvestri, 1912. At present, only six *Stygiocampa* species are known, and they are all cave-adapted and inhabit caves in Dinaric Mountains and western Stara Planina (Condé 1947, 1959, Condé and Bareth 1996, Denis 1923, Sendra et al. 2020, Silvestri 1931). Such macrosetae reduction is noticeable in *C. irakleiae* sp. nov. too, where there are no macrosetae either on mesonotum or metanotum; this absence was only seen in *Plusiocampa* (*Stygiocampa*) *christiani* Condé and Bareth 1996, from caves in Beljanica Mountains in eastern Serbia. Several important differences separate *C. irakleiae* sp. nov. from *P.* (*S.*) *christiani* and all *Stygiocampa* species, such as the thick barbed lateral pretarsal process of *C. irakleiae*, the smooth and setiform in *Stygiocampa*; the femora with one dorsal macrosetae in *C. irakleiae*, which are absent in *Stygiocampa* (Figs 15–16, 18). *C. irakleiae* has some resemblance with some of the *Stygiocampa* species, such as the small coniform appendages of the first urosternite, the extra number of urosternal setae, and the shape of urosternal macrosetae and stylar setae noticeably barbed. Whichever were to be the closest relation of *C. irakleiae*, we suggest that it is either close to Plusiocampinae, without medial posterior thoracic macrosetae as species of *Stygiocampa*, *Venetocampa* Bareth & Condé, 1984 subgenera, *Patrizicampa* Condé, 1962 genus and some species of *Plusiocampa* s. str. Silvestri, 1912 subgenus with paleobiogeographical consequences (Sendra et al. 2020).

Paleogeography and geological setting of Irakleia and its colonization

While the Aegean area is now extensively fragmented by the sea, it was part of a continuous landmass (Ägäis) during the upper and middle Miocene (23–12 Mya) (Dermitzakis and Papanikolaou 1981). After the collision of the African and Arabian Plate with the Eurasian Plate at the end of the Middle Miocene, a sea channel (Mid-Aegean trench) started to form and fully completed during early late Miocene (10–9 Mya), causing the separation of the Aegean islands into western and eastern groups (Creutzburg 1963, Dermitzakis and Papanikolaou 1981). After the Messinian crisis (6–5.3 Mya), when the Mediterranean basin dried up, and the opening of the Strait of Gibral-

tar (5.33 Mya), the Atlantic Ocean refilled the basin and islands formed again (Krijgsman et al. 1999). For the next 3 Mya, further sea expansion and landmass isolations took place in the Aegean. During Pleistocene orogenetic, eustatic, and volcanic events resulted in a continuous changing of the landscape and formation of several islands.

The Cyclades plateau was part of Ägäis and its complex geological and palaeogeographical history. The most recent fragmentation of the Cyclades plateau started at the last glacial maximum (LGM, 23–18 ka; Van Andel and Shackleton 1982, Lambeck 1996, Perissoratis and Conispoliatis 2003, Lykousis 2009). During the maximum of the LGM a major drop in the sea level (115–130 m) created a large insular landmass (Cycladia) of approximately 6,000 km^2 and several versions of the recent islands belonging to the modern Cyclades. By the beginning of the Holocene, Cycladia was replaced by new islands with small land-bridge between Greater Paros and Naxos. Irakleia was one of the last islands separated from Mikres Cyclades a few thousand years ago (Fig. 25).

The Irakleia island is dominated by a thick sequence of variegated and white calcite marble interleaved with mega-boudins of dolomitic marble (Seckel 2004, Behrmann and Seckel 2007). Metapelitic-schists intercalated with marbles are exposed on the central and southwestern parts of the island, while numerous metabauxites and laterites are preserved at the top of the thick sequence of the variegated marbles in the northwest part of the island (Brodhag et al. 2003, Seckel 2004, Behrmann and Seckel 2007). The main lithological units from bottom to top (Laskari 2018) include a) a basement of quartz-mica schists interlayered with lenses of orthogenessic bodies, which is underlying all other layers and is exposed only in the centre and southern part of the island; b) white ultramylonitic marble overlain by a thick sequence of coarse-grain variegated marble covering most of the island, c) quartz-mica schists intercalated with thin bedded marble exposed in the eastern part of the island, and d) Neogene sediments, which comprise mainly sandstones with cross-bedded layers and conglomerates. As in the rest of the Cyclades islands and in continental Greece (Riedl and Papadopoulou-Vrinioti 2001), the Plio/Pleistocene – Late Pleistocene generation of karst basins dominate in the Irakleia island (Figs 26, 27). An earlier colonization of Ägäis by the ancestors of *Cycladiacampa irakleiae* from Eastern Laurasia was possible and they dispersed on the European islands since the Eocene–Oligocene, when the closing of the Turgai Strait allowed the European–Asian connection (Decourt et al. 2000). Before this period, the western European islands were occupied by Campodeinae (*Podocampa* Silvestri, 1932 and *Litocampa* Silvestri, 1933 genera) and the tachycampoid phyletic group that still survives mostly in the Iberian Peninsula, Occitania region and western Mediterranean islands (Sendra et al. 2020). The wave of these ancestors without medial posterior thoracic macrosetae, would include the subgenera *Stygiocampa*, *Venetocampa*, the genera *Patrizicampa*, and *Cycladiacampa* and part of the *Plusiocampa* s. str. subgenus. These taxa probably descending from this first dispersal wave are currently distributed in the Dinaric Mountains, the isolated carbonate platform in Apulia (Italy) and the later-fragmented eastern microplates of the Iberian Peninsula (Sendra et al. 2020), and in Irakleia, in the middle of the Aegean Sea. The Laurasian origin was recently explained

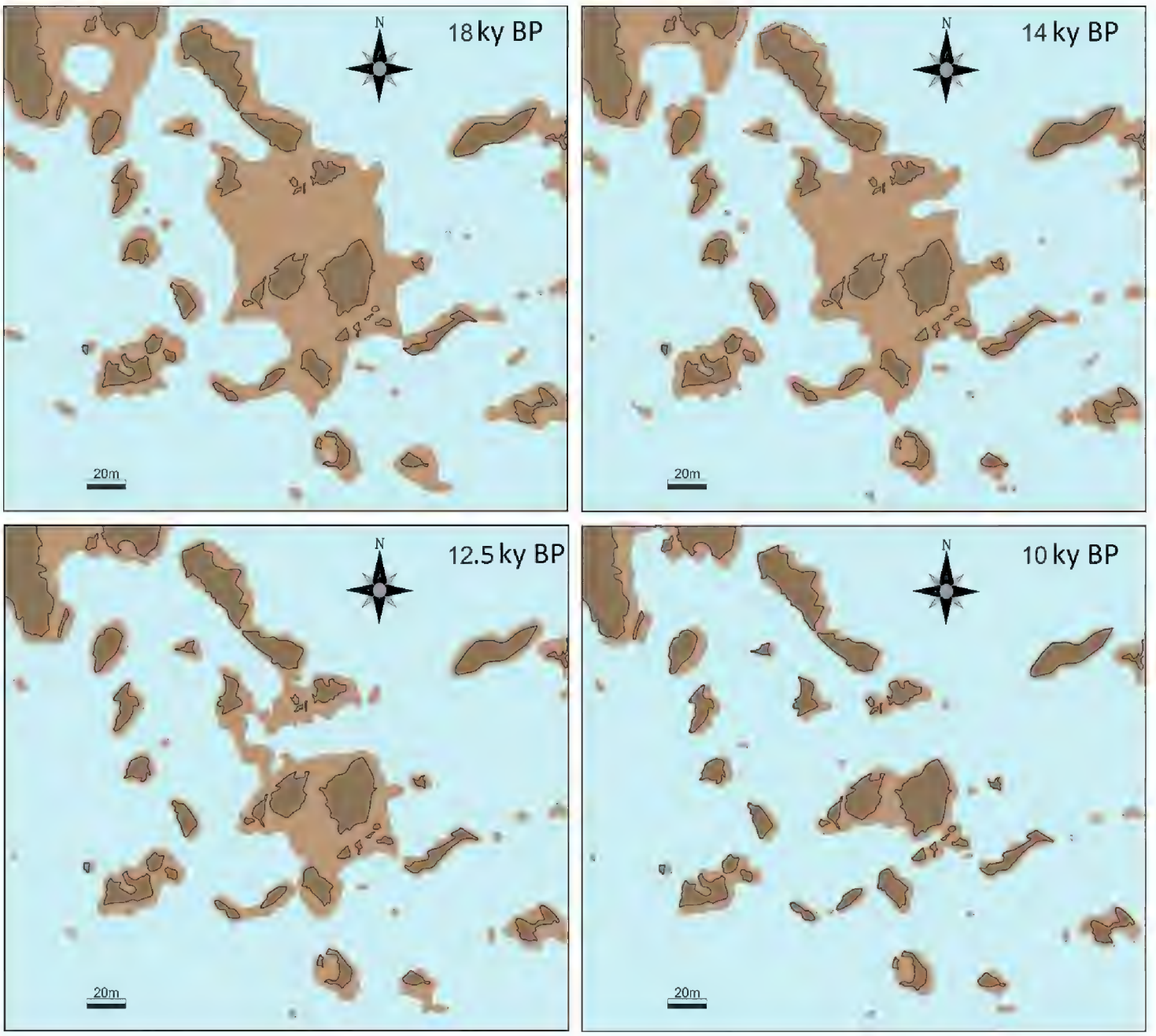
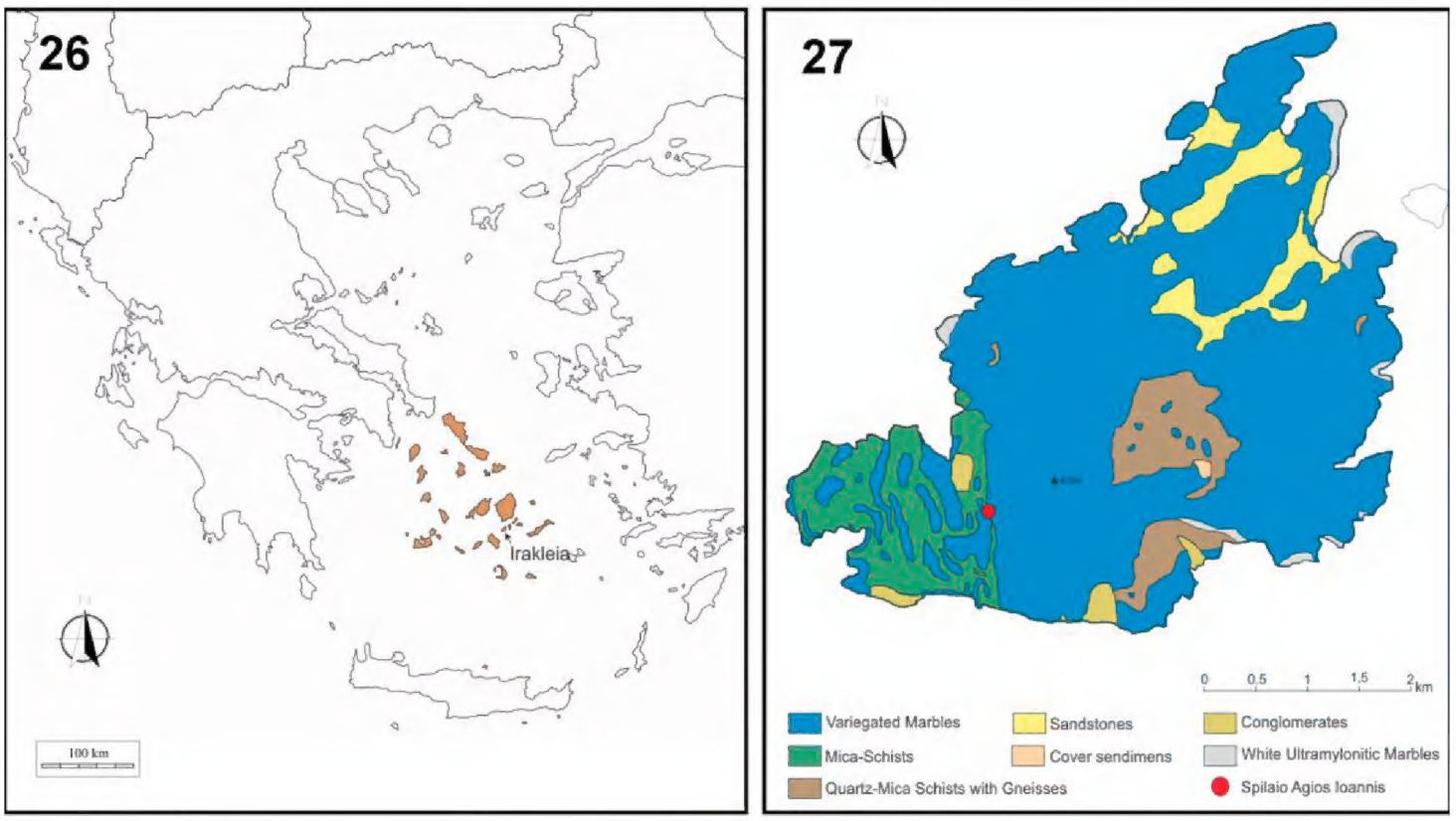


Figure 25. The fragmentation of Cycladia caused by the sea level rise followed the last glacial maximum (after Lambert 1996, modified).

by the newly found diversity of Plusiocampinae in Asia (Sendra et al. 2017; Sendra and Deharveng 2020). This distribution pattern is more evident for the cave-adapted species Plusiocampinae in the Euro-Mediterranean basin, and it highlights the phylogenetic proximity of *Stygiocampa* and *Cycladiacampa*. The presence of *C. irakleiae* is an unexpected surprise due to the periods of fragmentation of the Cyclades plateau and the isolation of the small short karst areas pin the Irakleia Island. A second wave of Plusiocampinae colonizers, with medial posterior thoracic macrosetae, could have entered through Anatolia during the Late Miocene, reaching the new lands on the Balkan Peninsula and the Aegean islands, Italian Peninsula, Rhône Valley, and Western Mediterranean, including the islands and the Pre-Baetic Mountains in the south of the Iberian Peninsula. This is the case for the six *Plusiocampa* species of the Aegean Islands, with the exception of *Plusiocampa* (*Plusiocampa*) *solerii* Silvestri, 1932, but including the two cave-adapted representatives recently described from Chios Island, *P.* (*P.*) *chiosensis* and Crete, *P.* (*P.*) *hoffmanni*.



Figures 26, 27. 26 Cyclades islands and the location of Irakleia **27** lithological map of Irakleia (redrawn from Laskari 2018).

Human activities and conservation

The presence of humans in the cave dates back to the beginnings of the Early Cycladic period (second half of the 4th millennium BC) and continues up to Modern time (Mavridis et al. 2018). The cave has been officially declared an archaeological site and is situated within the Wildlife Refuge "Nisos Irakleia" (OGG 1052/B/2000), the Special Area of Conservation "GR4220013 – Mikres Kyklades: Irakleia, Schoinoussa, Koufonisia, Keros, Antikeria Kai thalassia zoni", and the Special Protection Area "GR4220021 – Nisos Irakleia, Nisoi Makares, Mikros and Megalos Avelas, Nisida Venetiko Irakleias" (Law 3937/2011 & Joint Ministerial Decision 50743/2017)

Despite its legal protection status, the cave is not protected and several hundred people are visiting it every summer. The cave is dedicated to St John the Prodrome, celebrated every year on the 28th of August. We hope this contribution will raise awareness on the need to protect the cave due to, among other reasons, the exceptional importance of its cavernicolous fauna and the current addition of the remarkable new genus and new species *Cycladiacampa irakleiae*.

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